VISUAL ESTIMATION OF THE DIRECTION OF COMPLEX MOVING PATTERNS BY DOMESTIC CHICKENS (GALLUS GALLUS):

A BEHAVIOURAL ANALYTICAL APPROACH

A thesis

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Abstract

Humans and nonhuman primates are able to combine ambiguous directions of movement in a scene into a global motion percept and are able to solve the problem of estimating motion direction. There is extensive research on motion perception in humans, mammals and some avian species but little is known about the motion perception capabilities of the domestic chicken. We investigated whether domestic chickens are capable of determining global motion direction and developed methods whereby they were able to reliably indicate their direction estimates. A number of preliminary directional learning training conditions were used in order to teach the birds to selectively respond to moving patterns (sine wave gratings) which were moving in one of three directions (45°, 135° or 90°). Once this learning had occurred and was reliable, we presented 'plaid' probe trials which were summed gratings moving at 45° and 135°. Humans and nonhuman primates perceive this combined plaid pattern to be moving upwards at 90°. The experiments investigated whether the birds perceived upwards (90°) motion or the two diagonal directions separately when shown the plaid probe stimuli. The data show that the domestic chickens in our study were able to make directional judgements based on motion cues (they could reliably indicate 45° and 135° directions) but did not perceive the combined upward (90°) global motion as humans and nonhuman primates do. This suggests that they process visual motion differently from us.

Acknowledgements

I would like to thank both of my supervisors, John Perrone and James McEwan for their support and guidance through this research. To Jennifer Chandler, Rob Bakker and all of the students at No. 3 Dairy, this wouldn't have been possible without your help.

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Introduction

Vision and Motion Perception:

The ability to see the world around us comes from a complicated process of visual processing within the brain. Perhaps one of the most fascinating and complex phenomena that we can observe is motion perception. Most species who use vision as a primary sense are able to navigate their worlds effectively despite the overwhelming amount of visual information. For example, if we look at a crowd of people in a shopping mall there are multiple directions and speeds that people are moving at yet we manage to avoid collisions almost all of the time.

Figure 1: A still image representing how we perceive movement in a scene.

This motion perception is very important for locating and detecting danger (Bischof, Reid, Wylie, & Spetch, 1999). For example a moving leopard in the dense undergrowth of a forest is literally a black and yellow blur however due to

motion vision we know almost instantly that this is a dangerous situation. Although the image that our brain receives is a complex mixture of spots and lines moving in different directions, we are able to identify the overall direction of the leopard danger and decide our own actions accordingly. This is perhaps one of the best evolutionary advantages we can consider as most humans and prey animals are able to utilise this ability even when there is occlusion of an object with missing visual information (Hulme & Zeki, 2006). This process of combining multiple directions and speeds to create information is called global motion perception.

Global Motion:

We have the ability to sum up the various visual elements of a moving object in order to be able to see it as a moving entity. Mammals perceive motion due to the fact that specific neurons fire depending on the speed and direction an object is moving and the orientation of its edges (Pack, Livingstone, Duffy, & Born, 2003). Our brain then interprets this electrical information to create a perception of that scene or event. Once this neural chain of events has occurred we are able to take action, e.g., stepping out of the way, changing direction, or stopping.

Consider the crowd of people again; a large proportion of these people may be moving towards the exit. There are large differences in the speed, size and space between each individual, such that the neurons processing this visual motion information will be firing at completely different times and places resulting in a large amount of visual information for the brain to decipher. Yet, we are still able to determine the overall speed and direction of the crowd. We can detect the

overall global movement of the crowd despite the fact that the image motion generated in our eyes consists of many different directions and speeds. However staring at crowds is not an efficient or accurate way of studying this phenomenon so scientists have discovered far better ways of researching global motion through the study of moving patterns.

Pattern Motion:

Patterns containing a range of lines or edges of different orientations are widely used to research motion perception as they are subject to a phenomena known as the aperture problem (defined below) and can provide us with a test case for the study of global motion perception (also called pattern motion perception). The most common type of patterns consist of combinations of sine wave gratings. A single sine wave grating stimulus has an intensity profile that varies across the image in the form of a sine wave. They can be systematically varied in the separation of the light and dark bars (spatial frequency), the speed they move at (temporal frequency) as well as the amplitude of the intensity variation (contrast) and the orientation of the bars. These grating stimuli are used to study many aspects of motion perception such as contrast thresholds, motion after effects, acuity thresholds and flicker perception (Blake and Sekuler, 2006). A common stimulus for studying global motion perception is a single grating that moves behind a rectangular shaped window (this is often referred to as the 'barber pole'). Another very common stimulus for studying pattern motion is the 'plaid' (Movshon & Adelson, 1984). This is created by summing two or more gratings with different orientations and motion directions (See Fig. 3).

A lot of research into pattern motion perception comes from neurophysiological studies that determine what parts of the brain are active while animals are viewing moving patterns such as gratings or plaids (Movshon & Adelson, 1984, & Pack, et al., 2003.) These types of studies have revealed neural pathways and physical structures within the brain responsible for motion direction estimation and have provided insights into how global motion could occur in the primate brain.

Another style of research which is commonly used to study pattern motion is psychophysics. Psychophysics is the study of the relationship between physical characteristics of stimuli and the sensory experiences that accompany them (Baird, 2010). There is a vast array of research concerned with this type of experimental design and this is perhaps the oldest branch of experimental psychology (Colman, 2015). Psychophysical research does not always require verbal feedback from the subject which is why it is an ideal experimental design for non-human subjects. Researchers have used this style of experimentation to study aspects of vision such as the visual acuity of various species of mimicking birds in order to gain a better understanding into interspecies relationships. Studies such as this reveal clues as to how different animals learn mating behaviours and dominance (Prum, 2014).

Pattern and global motion perception is a widely researched area in the field of vision science and has been studied using a range of techniques. This thesis will use psychophysical techniques to study global motion perception in birds. It will examine a specific type of global motion estimation known as the aperture problem.

Aperture Problem:

A particular visual phenomenon that we face as humans is called the aperture problem. (Wuerger, Shapley, & Rubin, 1996). This is when we perceive the global, overall direction of a moving object incorrectly. It is caused by the occlusion of edges and end points causing misinformation and ambiguity of true direction (Piers & Livingstone, 2006).

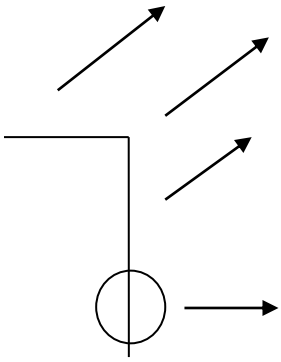
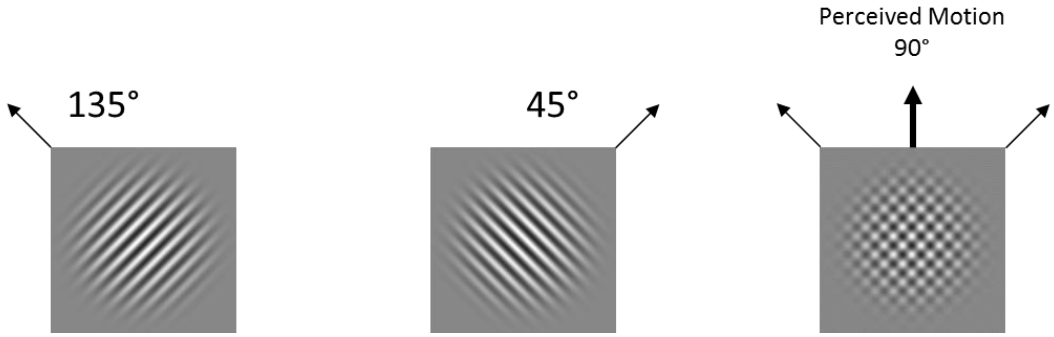


Figure 2: Represents the occlusion of edges when looking through an aperture resulting in the aperture problem.

A moving object that is only seen through an aperture will appear as though it is moving across that aperture in a direction which is not true to the overall correct movement. Consider *Figure 2* for example; the 2D corner is moving in a 45°direction but when viewed only through the small circular window (aperture) along the vertical edge, it will appear as though it is moving horizontally (0°). Only the motion orthogonal to the edge is visible; the motion along the edge cannot be detected and information concerning the true direction is lost. Motion seen through a small aperture is therefore ambiguous (hence the aperture problem) It is the occlusion of the entire moving object and the inability to see multiple edges in the aperture that results in the incorrect percept of an object's true direction of motion.

Our visual system views the motion of objects through many small apertures, namely the small, localised processing areas (receptive fields) of the cells specialized for motion in the brain. The circle in Fig. 2 could therefore represent the area of the retina sampled by a single motion sensitive neurone in the brain. Many such receptive fields tile the scene we are looking at and they are all analysing the motion that is occurring. The brain receives multiple signals about the motion of the edges making up an object and each small patch of the visual field is subject to the aperture problem. Yet we tend to perceive the correct overall motion of the moving objects. How this occurs in the brain and how we overcome the aperture problem is a major research question in the area of motion perception.



*Figur*e *3:* Still images representing sine wave grating patterns which are summed to produce a sine wave plaid. The actual grating and plaid stimuli used in the experiments are looped movie files.

Plaids:

A common test for probing how we solve the aperture problem is to present observers with the plaid stimulus shown in Fig. 3 above. When 135° and 45° moving grating patterns are presented separately we are able to accurately perceive the true direction (shown by the solid black arrows). When the two

moving gratings are summed to create a ‘plaid’ the stimulus contains two separate motion directions, yet we perceive the two gratings as a pattern moving in an upwards direction of 90°. The brain somehow combines the separate directions of motion into one global percept that is moving upwards. Each individual grating motion direction is in fact ambiguous because of the aperture problem. However, when combined, they form an unambiguous upward motion percept.

These stimuli contain multiple edges at different orientations. The ability to resolve and overcome the local direction errors elicited by complex stimuli containing multiple edges at different orientations and to estimate the correct overall ‘global’ direction of motion is due to the specialised cells in the human brain which can solve the aperture problem (Movshon & Adelson, 1982, & Pack, et al., 2003). Cells that are specialised for detecting edges, direction, and line terminators are present in the mammalian brain (Beer, Watanabe, Ni, Sasaki, & Andersen, 2009; Gharaei, Tailby, Solomon, & Solomon, 2013; Hubel & Weisel, 1968; Kourtzi, Krekelberg, & van Wezel, 2008). Cells specialised for motion direction and which seem to be involved with solving the aperture problem (global motion perception) are located in the extra striate visual cortex in the middle temporal (MT) area also known as V5 (Cheadle & Zeki, 2014; Movshon & Adelson, 1984; Schlack & Albright 2007, Zeki & Stutters, 2013).

The human and non-human primate visual systems are well understood and much of the research on the aperture problem has been conducted on these species. Little research has been done on global motion perception within other species such as birds although there is a large portion of research more broadly focused on motion perception in general within avian species.

Motion Perception in Birds:

Random dot displays are another common stimulus used to study motion perception. These types of experiments require the subject or participant to provide feedback on the direction of dots moving in a range of directions and to decide if there is an overall global direction to the moving pattern of dots. In these random dots experiments the ability to determine directions is found by measuring the 'coherence threshold' which is the lowest percentage of dots that can move in a particular direction versus random directions and still elicit a correct direction response. Bischof et al., (1999) conducted research which compared human performance against that of pigeons. They found that humans are much better at perceiving motion from random dot movement and can do so in the presence of a lot more dynamic noise. The researchers attribute the performance differences to a weaker spatiotemporal motion integration system in pigeons. Oddly enough, this suggests that pigeons do not have the motion perception abilities of humans even though they are able to fly, a task which one imagines involves complex patterns of visual motion information. It is suggested that pigeons are able to carry out this complex flying task by utilising a system which works very well at organising motion involving large amounts of movement and pattern directions at a time (Wylie, Bischof, & Frost, 1998).

Motion perception has also been studied by recording the neural activity in pigeons. The birds viewed computer generated moving dot displays in which the dots could vary in both size and speed. The results of this research imply that pigeons have specialised cells that are used when detecting what's called motion parallax. Motion parallax is the term which describes how we perceive objects which are closer to us as moving faster than objects which are further away.

Electrophysiological studies have recorded the neural activity during trials in which motion parallax stimuli were shown to pigeons and this showed that specific neurons fire for stimuli that were perceived as near and separate neurons fired for stimuli that were perceived as far away (Xiao & Frost, 2013).

As previously mentioned primates have neurons (Middle Temporal or MT) which have evolved specifically for determining the direction of motion patterns (Movshon & Adelson, 1984). Baron, et al., (2007); Pinto, Lima, & Neuenschwander, (2007); Bingman, Gasser, & Colombo (2008); Karten, Hodos, Nauta, & Revzin, (1973); Macko & Hodos, (1984) suggest that the equivalent motion processing neurons in the avian brain are called Wulst cells. These are similar in that they are directionally selective, although not sufficient for determining global motion as seen with the moving plaids. Baron et al., (2007), Pinto, Lima, Neuenschwander, & Baron, (2006, 2007) tested this theory by observing the neural activity in barn owls when presented with a computer generated plaid stimuli. This strongly suggests that avian species detect motion in a similar fashion to primates as they have motion detecting cells, or the equivalent, although the structure of the visual system may be slightly different (Xiao & Frost, 2013).

Avian Vs. Mammalian Motion Perception

The fact that motion based experiments have been conducted using avian species such as owls, other predatory birds and specifically pigeons, also implies that other members of the species will be suitable for research of this kind (Zahar, Wagner, & Gutfreund, 2012).

One of the main physiological differences between non-predatory birds, such as pigeons, sparrows and chickens, and humans is the placement of the eyes on the head. Humans gain their depth perception due to two forward facing eyes which have overlapping visual fields, whereas these species of bird have laterally positioned eyes (Goldstein, 2002). The human visual system is able to account for the differences in distance of objects from each eye using a method called binocular matching. This is the visual system's ability to account for the spatial differences between an object and each eye which is made easier by the binocular placement of our eyes. The lateral placement of chickens' eyes, and many other non-predatory birds' eyes makes the use of binocular cues more difficult although motion direction, speed and orientation are all relevant cues which could also be used to aid in depth perception (van Ee & Anderson, 2001).

This difference in eye placement can be understood better by studying skills such as depth perception and a number of experiments have been conducted on this using birds (O'Brien & Johnston, 2000). Predatory birds do not have laterally placed eyes as do non predatory birds. We can infer that they rely far more on the use of binocular vision than these forage-feeding birds. Locating and tracking prey from a distance is not a priority for birds such as pigeons and chickens which is why they have evolved laterally placed eyes more specialised in taking food at the bill and taking food at the feet (Martin & Katzir, 1999). Nonetheless, these forage-feeding birds still navigate the world successfully which requires a high level of motion perception abilities.

Specialised selective cells have been labelled differently between birds and mammals yet they are located in similar visual areas. Although the visual systems are different, the final product of perception appears to be similar between most

mammals and birds. Thresholds and performance may vary across visual tasks depending on the needs of the species. Whether there is colour, acuity, or threshold differences interspecies, vision is still a very important sense for many of the fore mentioned species. We have a basic understanding of the perceptive capabilities of a lot of different species of birds but little is known about the Domestic Chicken (*Gallus gallus*).

Domestic Chicken Vision:

Many animals use vision as a way to perceive their world and locate, identify and track both points of interest, such as food, and crucially, danger. Domestic Chickens (*Gallus gallus*) are thought to have well established vision along with many other species of bird which can be inferred from their behaviour (Dawkins, 2002).

Domestic Chickens view their world using single lens eyes which are located laterally on their head. This type of eye placement on an organism's head gives us information on what type of vision a species has, but also the strengths and weaknesses their visual processing systems have along with how much emphasis vision has amongst their other senses (Dawkins, 2002 & Dawkins & Woodington, 2000).

The lateral placement of the eyes provide chickens with a wider range of vision than a human but impacts on their depth perception (Kral, 2003). Birds with laterally placed eyes may lack this ability since humans gather much of their depth perception from stereopsis and forward facing eyes (Goldstein, 2002). This suggests that chickens use different sections of the eye for viewing different

objects in their environment. Research indicates that the binocular field of view may be associated with locating food and pecking behaviours while lateral viewing may be used for more movement based perception (Dawkins 1995, 1996, 2002; Maldonado, Maturana, & Varela, 1988). There is still much about the chicken's visual system that is not well understood and one of the aims of this thesis was to gain greater insight into the way they process visual motion information. Based on previous research, chickens may perceive their world differently from humans and other mammals. Structurally their eye and visual systems are different which may impact how they deal with motion perception phenomenon such as the aperture problem. Previous research in this area has largely focused on humans or gathered neurophysiological data from various animals.

Nonhuman perception research has provided us with a vast array of knowledge when we look at different species' abilities and processing mechanisms (Blake, 1998 pp26 as cited in Blake & Sekuler, 2006). By conducting research on chickens, we may uncover certain physiological or behavioural features which help us better understand how visual perception works across many species. This thesis looked at one particular aspect of chicken vision, namely how motion direction information is processed by the domestic chicken's visual system.

Our Objectives

This thesis will try to determine whether the Domestic Chicken has the ability to detect the correct global motion from a combined pattern made up of two separate motions (aperture problem). This will be tested using a common grating/plaid

based stimuli (see Fig. 3) presented to the subjects on a screen. The challenge is to train the birds to reliably identify and discriminate between three motion directions such as 135°, 90°and 45°. This will then enable probe trials to be introduced that show a moving plaid pattern which we tend to see as moving upwards (90°) and see how the birds respond. If they perceive the plaid patterns as we (and other non-human primates) do, they should select the vertical direction. This will indicate that they are able to combine the two separate grating directions (135°and 45°) into one global pattern motion direction.

This thesis will therefore focus on providing our subjects with a reliable language in which they can relay feedback to us. Can they reliably indicate when the grating is moving at 135°and not 45°? How much training is required to get them to an adequate level of performance? By monitoring response performance we will actively modify the experimental methods until we are satisfied that the responding is adequate for the next level of learning. In doing so we will be able to gain a better understanding of how to train and use domestic chickens for experiments testing their visual capabilities.

As previously stated, psychophysical research is a common and robust method of experimental design for studying perceptual skills such as vision. However it is often a challenge when used in non-human studies and many research papers often fail to report that the researchers had difficulty reaching the desired performance from their subjects. This is partly due to the training processes used during initial phases of this type of research which are seldom included in the final publications. A lack of communication about different approaches to training can result in the use of many different techniques which may not work effectively. The emphasis in this thesis will be in the development of good training methods

suitable for future studies of the perceptual skills of domestic chickens. Chickens are readily available at the animal facility at the University of Waikato and provide a convenient means for the study of bird vision.

This thesis will aim to achieve two goals. Develop a reliable method in order to achieve the desired performance from the subjects using a range of behavioural analytic techniques. By utilising a behavioural analytic approach we will prepare the subjects for the work demanded of them and we will constantly adjust our methods to fit the performance requirements. By developing a reliable method of training this thesis will seek to achieve the second goal: teaching and maintaining performance at a level high enough to present the plaid probe trials in the 135°, 90°and 45° direction discrimination task described above. By achieving the required subject performance and presenting ‘plaid’ probe trials, we hope to determine whether or not the domestic chicken has the ability to overcome the aperture problem.

Method

Subjects

Subjects were three mixed breed domestic hens (*Gallus gallus domesticus*) numbered 13.1, 13.2, and 13.3, along with three mixed breed domestic roosters (*Gallus gallus domesticus*) numbered 13.4, 13.5, and 13.6, varying in age at the start of the experiment. All subjects had previous experience in a chamber, some more than others, and had been trained using wheat in other behaviour-based experiments. However, all six subjects had never had any previous experience on a digital screen-based experiment.

Chickens were housed individually in a room with up to 36 chickens with free access to water and appropriate vitamins and medication is available from the staff. Chickens were restricted on food intake during experiment times but were weighed and fed depending on what was appropriate.

All procedures complied with the University of Waikato's Animal Ethics Committee requirements.

Apparatus

During the experiments chickens were individually removed from their cages and put into an operant chamber which was approximately 800mm wide, 500mm high and 500mm deep. The chamber included a screen which presented stimuli for the hen to peck which triggered a hopper of grain for correct responses. The feeding magazine was available for 3 seconds and mechanically shifted the feeder forward

for the chickens to access wheat. An infrared device was triggered when a subjects head broke the beam to gain access which was recorded by the experimental software.

A Dell screen measuring 1024 x 768 pixels (270mm x 203mm, model number 710A) was installed above the magazine aperture. Pecks to the screen were recorded as x, y co-ordinates. Response keys consisted of two circles positioned at (x, y) = (125, 825) pixels (left key) or (1075, 825 pixels) (right key). Each key could be either red or green and its intensity profile was based on a 2-dimensional Gaussian function with a standard deviation of 40 pixels. Stimuli were created using custom Matlab code and saved as .avi format, and designed to run at 60Hz.

A Dell computer (Optiplex model 780) running a custom-made application controlled the experimental programme. Data recording was event-driven, and session data was also recorded manually.

Training

Subjects were weighed before each experimental session and then placed in the chamber. As subjects had no prior experience of a screen-based experiment, training was conducted using backward chaining where initially an FR1 procedure was put in place for the red response key on the right of the screen. Reinforcement was gained immediately after a peck within the adjustable peck radius of a response key. All birds were reliably pecking the stimulus after two training sessions on different days and were then moved onto the next condition.

Condition 0.1 consisted of a looped movie of a sinewave grating pattern (512 x 512 pixels) moving from left to right (0°) which was presented in the middle of the screen against a solid light grey background (see figure 3). Two more training days were required for reliable pecking of the grating followed by the red key. This was achieved using hand shaping by bringing the food magazine forward manually for successive approximations of the target behaviour.

Condition 0.2 was a repetition of the previous condition but instead had a left moving grating pattern (180°) which was followed by a green key located to the left of the screen. This condition was mastered in only one session and the birds were then moved onto the next training condition.

Condition 0.25 was simply a mixture of the two previous conditions where only the correct key was presented after a grating peck. Trials would be presented pseudo-randomly either 0° or 180° and a peck within the peck radius would result in the presentation of the correct key. This was to ensure the subjects did not develop a bias for either key.

Conditions 0.3 - 0.5 are detailed in *Table One* which summarises the condition type along with the amount of days each subject spent on the various conditions. Further details on the subjects' performance during each condition will follow.

It is important to note the variation in condition participation for Bird 13.5 as the subject was replaced during the early training stages due to poor performance. The replacement bird shows less training days in general per condition and also the absence of conditions 0.3, 0.5 and 0.15. This is due to a streamlining of the

training procedure and also the rapid acquisition of new skills from the replacement bird.

Condition Number	Bird Number	Days on Condition
Cd 0	N/A	N/A
Cd 0.1		
Cd 0.2		
Cd 0.25		
Cd 0.3 0°-180° w/ green and red	13.1	15
	13.2	15
	13.3	14
	13.4	15
	13.5	N/A
	13.6	12
Cd 0.4 Adjusted to 45° and 135°	13.1	11
	13.2	6
	13.3	4
	13.4	11
	13.5	5
	13.6	6
Cd 0.5 90° Yellow introduced	13.1	7
	13.2	12
	13.3	11
	13.4	6
	13.5	N/A
	13.6	11
Cd 0.15 90° Yellow presented alone	13.1	4
	13.2	3
	13.3	3
	13.4	3
	13.5	N/A
	13.6	3
Cd 0.31 90° yellow vs. 135° green	13.1	8
	13.2	7
	13.3	8
	13.4	8
	13.5	11
	13.6	8
Cd 0.32 90° yellow vs. 45° red	13.1	32*
	13.2	21
	13.3	20*
	13.4	29*
	13.5	14
	13.6	39*
Cd 0.5 All three direction and keys	13.1	52*+
	13.2	43*
	13.3	43*
	13.4	36*
	13.5	37*
	13.6	27*

Table One: Summary of Time Spent on each Condition

* indicates where a ratio of 2:1 or higher was introduced at some stage to try and increase performance on the yellow key.

+ indicates that the subject never progressed with the experimental condition due to a lack of mastery.

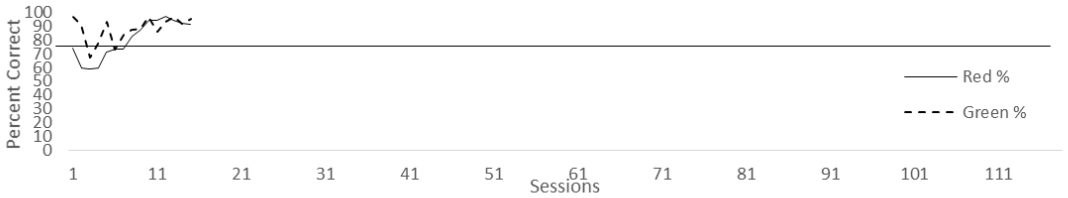


Figure Four 13.1 Condition 0.3 Total Data

Figure Five 13.2 Condition 0.3 Total Data

Figure Six 13.3 Condition 0.3 Total Data

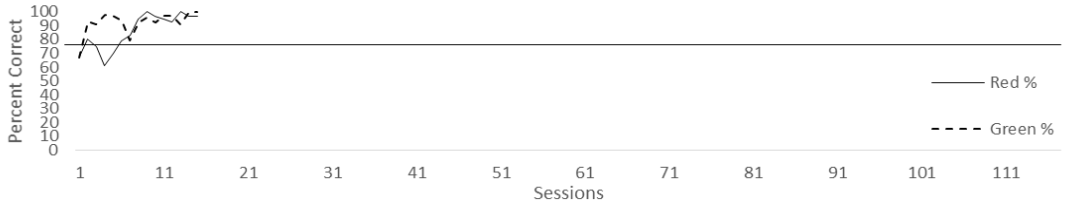


Figure Seven 13.4 Condition 0.3 Total Data

Figure Eight 13.5 Condition 0.3 Total Data

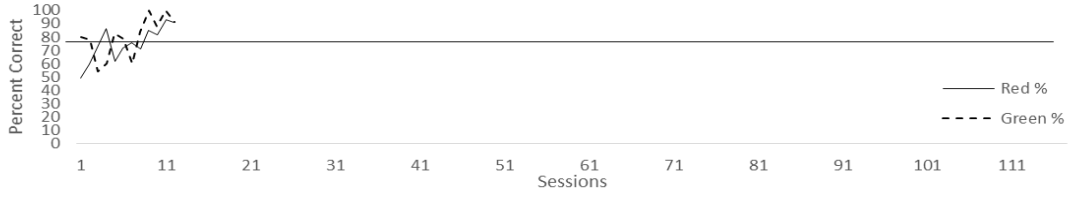


Figure Nine 13.6 Condition 0.3 Total Data

Condition 0.3

Condition 0.3 required the subjects to acquire knowledge of the direction of the grating pattern and then correctly peck the corresponding key when both were presented. This procedure ensured that the subjects were using the direction of motion as a cue rather than the orientation of the bars within the grating patterns. Again, trials were pseudo-random and could be either 0° or 180° moving grating patterns. It was important to establish the association between the movement direction cues and the correct keys in order to progress through the training as the main experimental conditions required a high standard and maintenance of these skills.

Training condition 0.3 (*Figures 4-9*) show overall performance when subjects were presented with pseudo-random trials of 0° or 180° moving grating patterns and both response keys. Mastery was achieved once the subjects obtained percentages of 75% or above over two consecutive days.

Once this condition had been conducted the subjects were then able to move onto the next condition (0.4) in which the angle of gratings were adjusted to 135° or 45°. Since these were the angles of the gratings making up the plaid stimuli to be used in the main experiment it was important that they could reliably discriminate and report on these two directions.

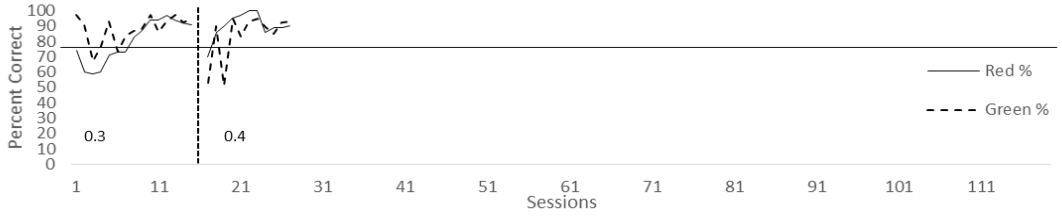


Figure Ten 13.1 Condition 0.4 Accumulative Data

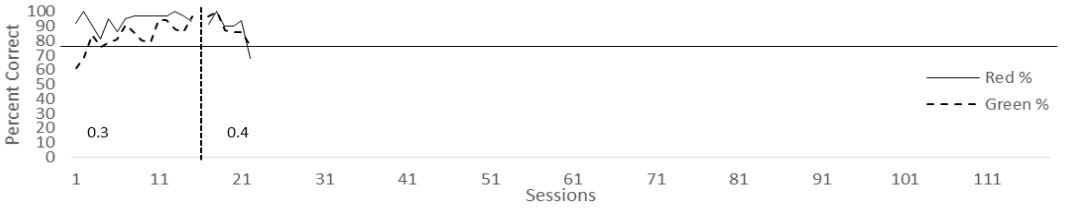


Figure Eleven 13.2 Condition 0.4 Accumulative Data

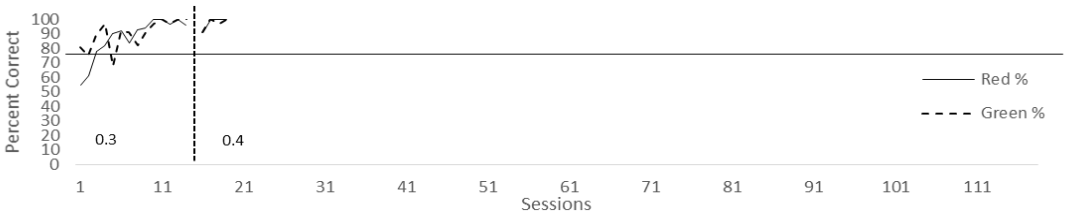


Figure Twelve 13.3 Condition 0.4 Accumulative Data

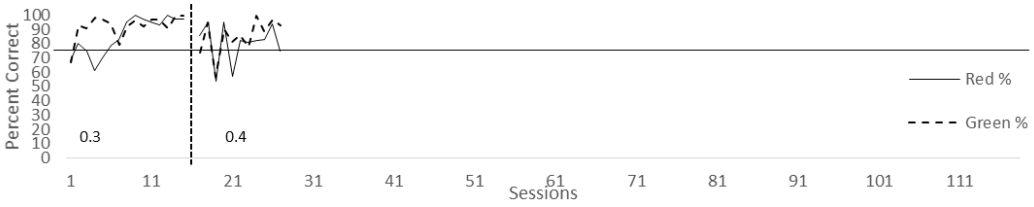


Figure Thirteen 13.4 Condition 0.4 Accumulative Data

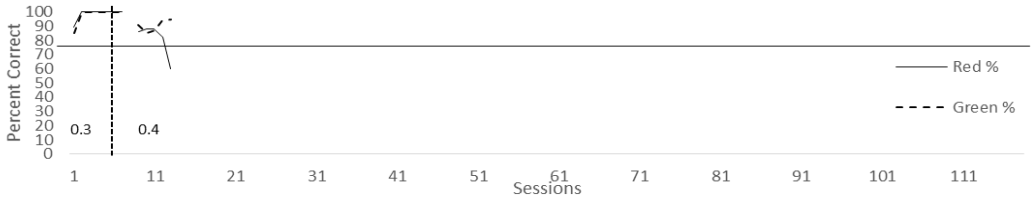


*Figure Fourteen*13.5 Condition 0.4 Accumulative Data

Figure Fifteen 13.6 Condition 0.4 Accumulative Data

Condition 0.4

Training condition 0.4 (*Figures 10-15*) show overall performance when subjects were presented with pseudo-random trials of 135° or 45° moving grating patterns and both response alternatives (same red and green keys as previous conditions but now adjusted to sit at 135° or 45°). Successful performance was achieved once the subjects obtained percentages of 75% or above over two consecutive days.

Mastery on the 135° versus 45° condition led to the addition of another grating pattern with an additional response key alternative. By adding in a grating which moved vertically upwards (90°) tied to a yellow key response option (located above the grating stimuli at 90°) we hoped to train performance on the direction critical to the plaid experimental phase; if the birds perceived the overall global motion of the plaid they should see it moving in the 90° directions and respond mainly with the yellow key.

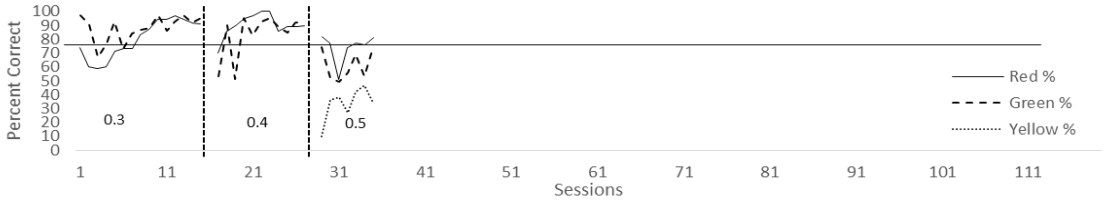


Figure Sixteen 13.1 Condition 0.5 Accumulative Data

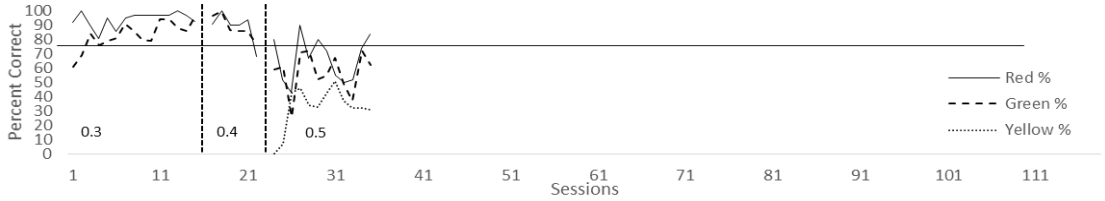


Figure Seventeen 13.2 Condition 0.5 Accumulative Data

Figure Eighteen 13.3 Condition 0.5 Accumulative Data

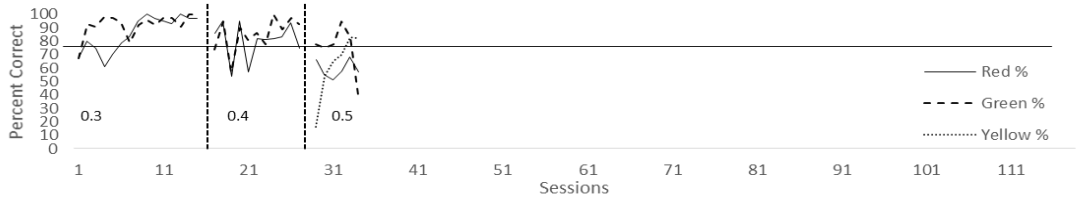


Figure Nineteen 13.4 Condition 0.5 Accumulative Data

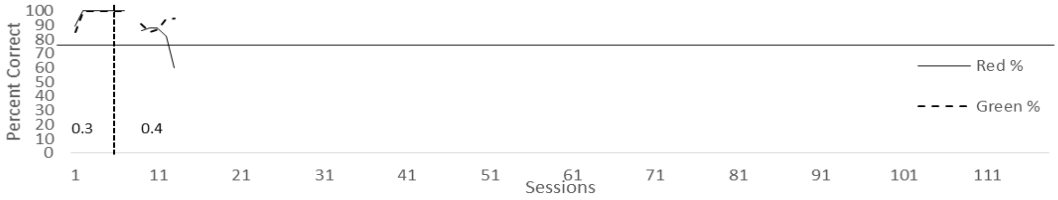


Figure Twenty 13.5 Condition 0.5 Accumulative Data

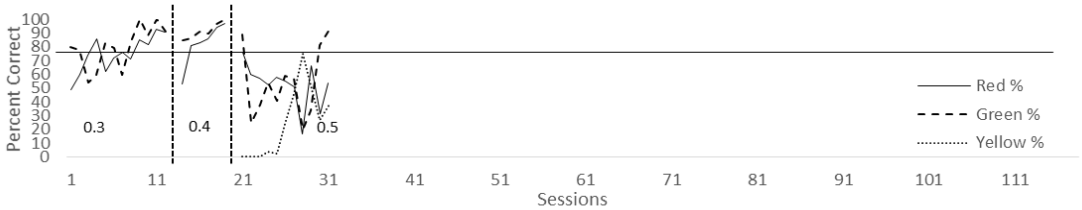


Figure Twenty One 13.6 Condition 0.5 Accumulative Data

Condition 0.5

Condition 0.5 (*Figures 16-21*) shows overall performance for all trials when presented with the previously mastered directional gratings (135°, green key) and (45°, red key) along with the new stimulus (90°, yellow key).

Performance on all keys rapidly declined with the addition of the new response alternative so the presentation of a 90° grating and yellow key alone condition was designed to teach pairing between upwards movement and yellow key along with access to food. This condition did not require data collection as the subjects were only presented with 90° grating stimuli and the correct response stimuli (yellow key). 3-4 days was required to build a strong association with the pattern direction and appropriate response.

The next two conditions were designed in order to pair the new stimulus (90° grating, yellow key) with one of the previously mastered keys at a time to try and improve performance.

Condition 0.15

Condition 0.15 consisted of 3-4 days presenting yellow key alone after a 90° trial in order to establish pairing between the new key and the direction along with access to reinforcement.

Once this association was formed the next two conditions were created and required performance on the previously mastered keys along with presentations of the new upwards grating.

Condition 0.31

The first new condition consisted of 135° gratings (green key) randomly presented amongst 90° (yellow key) trials. Figures 22-27 represent the data obtained during this condition.

Mastery was obtained once there were two consecutive days above 75% correct on both keys. Once this was achieved the subjects were moved onto the alternate pairing of yellow trials and side key trials.

Condition 0.32

Condition 0.32 involved random trials of 90° gratings (yellow key) and the opposite angled grating, 45° (red key). Figures 28-33 represent the data obtained during this condition. Mastery was obtained once there were two consecutive days above 75% correct on both keys.

Successful learning on these two conditions meant that the subjects were ready to be presented with the final training condition which would consist of mixed trials of all three grating types.

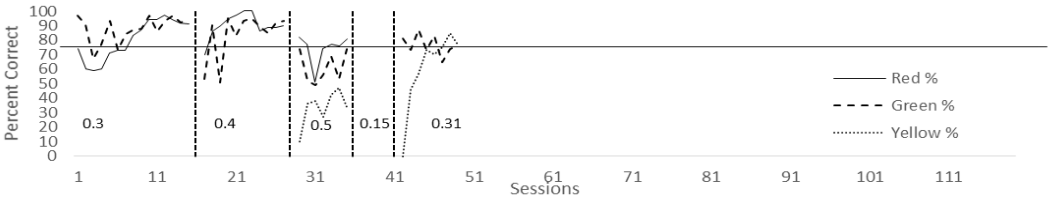


Figure Twenty Two 13.1 Condition 0.31 Accumulative Data

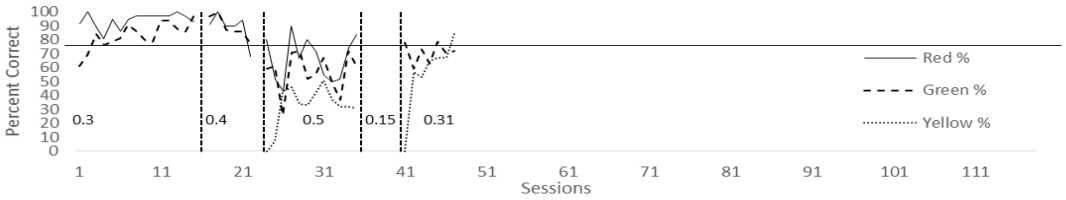


Figure Twenty Three 13.2 Condition 0.31 Accumulative Data

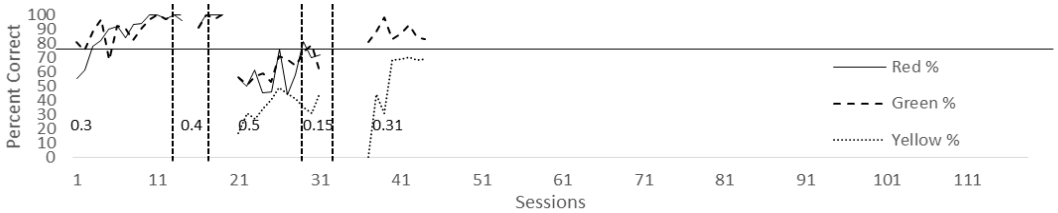


Figure Twenty Four 13.3 Condition 0.31 Accumulative Data

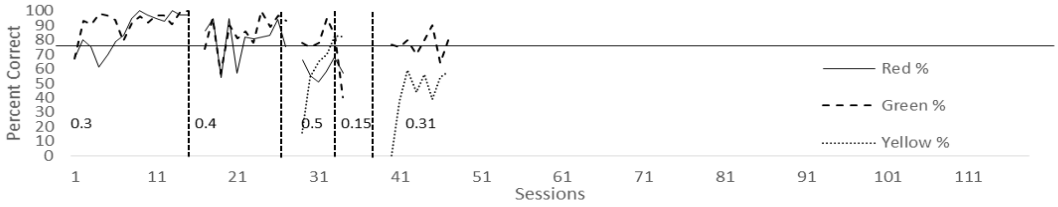


Figure Twenty Five 13.4 Condition 0.31 Accumulative Data

Figure Twenty Six 13.5 Condition 0.31 Accumulative Data

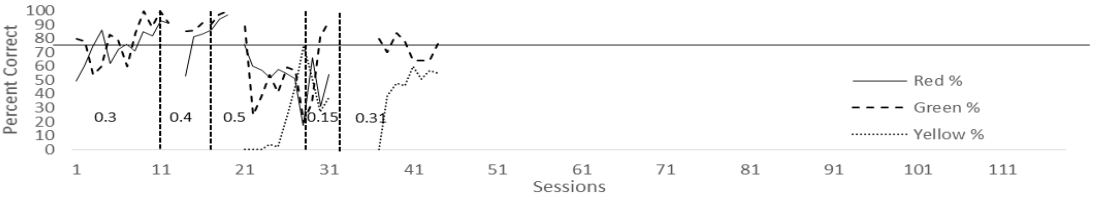


Figure Twenty Seven 13.6 Condition 0.31 Accumulative Data

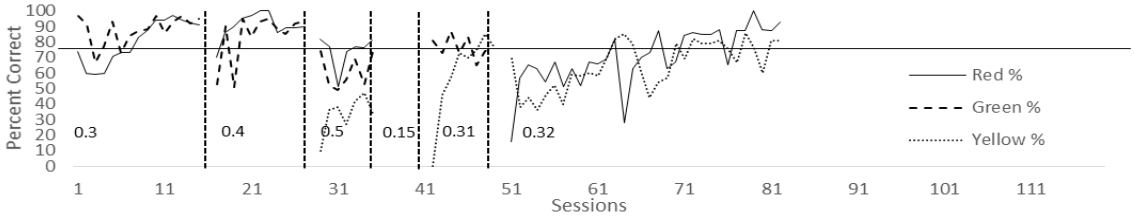


Figure Twenty Eight 13.1 Condition 0.32 Accumulative Data

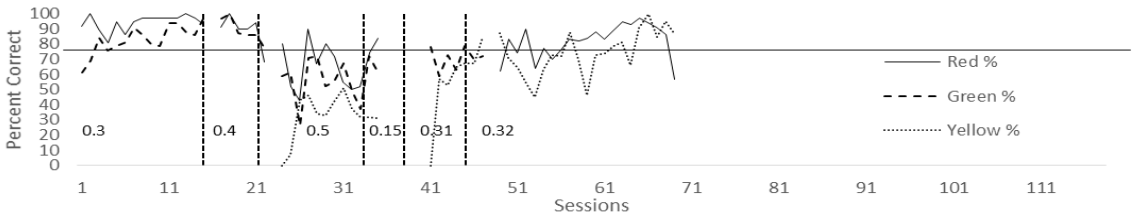


Figure Twenty Nine 13.2 Condition 0.32 Accumulative Data

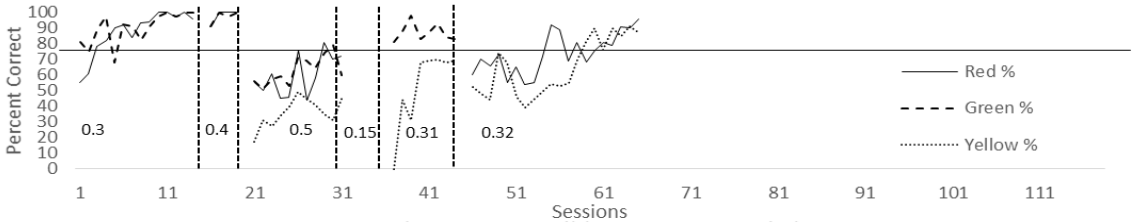


Figure Thirty 13.3 Condition 0.32 Accumulative Data

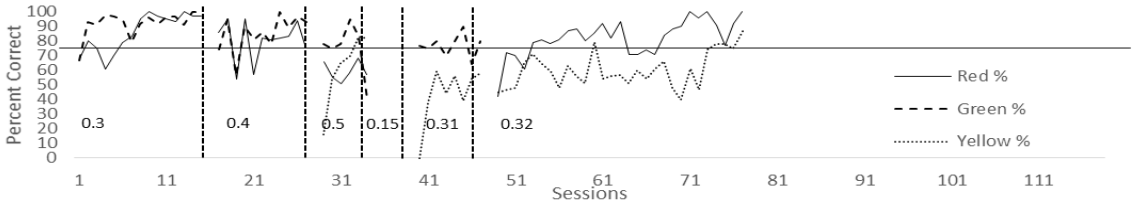


Figure Thirty One 13.4 Condition 0.32 Accumulative Data

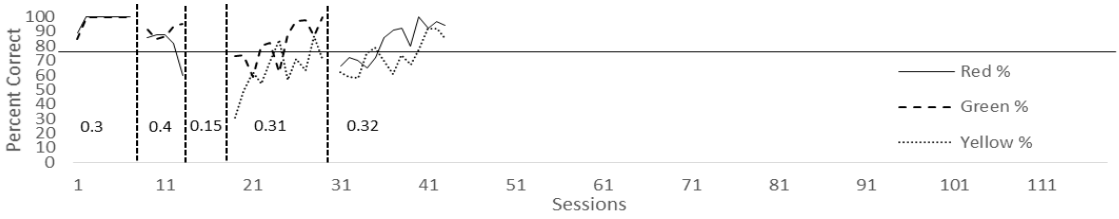


Figure Thirty Two 13.5 Condition 0.32 Accumulative Data

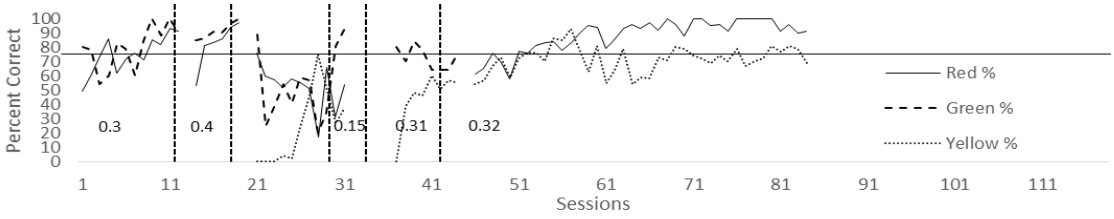


Figure Thirty Three 13.6 Condition 0.32 Accumulative Data

Conditions 0.31 & 0.32

Figures 22-27 show the data obtained for Condition 0.31. 90° (yellow key) trials were increased at 2:1 or 4:1 ratios (see *Table One)* to try and increase performance. Responding was deemed accurate once the subjects ceased to fluctuate greatly across sessions and began to plateau at a reasonable level of performance during Condition 0.31. Although the performance threshold had previously been 75% over two consecutive days the decision was made to have a more loosely based threshold as the next condition (Condition 0.32) involved a continuation of the presentation of 90° grating and yellow key, which was the pairing that the subjects were having difficulty mastering.

Having previously mastered the side keys, these two conditions maintained 135° (green key) and 45° (red key) performance whilst integrating the 90° (yellow key) stimuli.

The graphs show (*Figures 22-27* Condition 0.31 and *Figures 28-33* Condition 0.32*)* a gradual increase in performance over the pairings of green and yellow and red and yellow.

The next level of training was designed to present all three alternatives in order to integrate performance over all three stimulus types just as the previous Condition 0.5 tried to do. Although this condition had been conducted earlier, performance was now trained methodically to try and produce better performance.

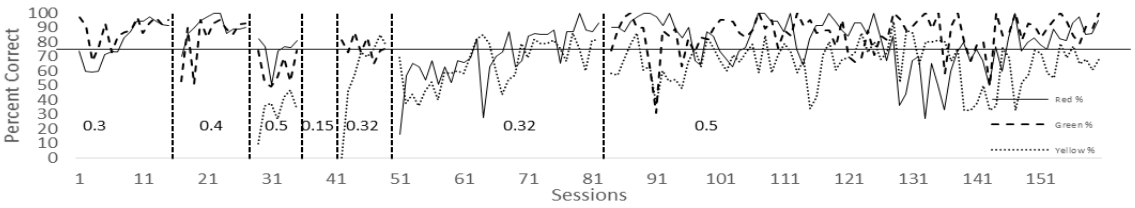


Figure Thirty Four 13.1 Condition 0.5 Accumulative Data

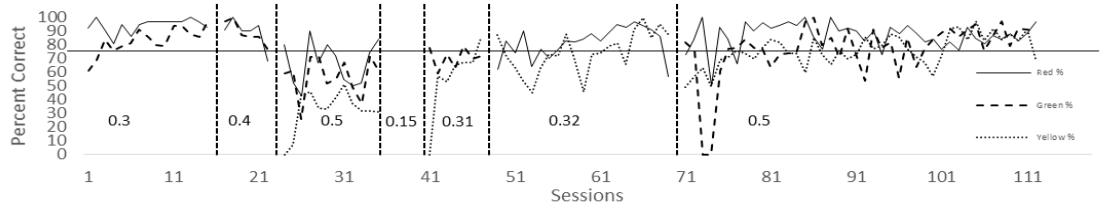


Figure Thirty Five 13.2 Condition 0.5 Accumulative Data

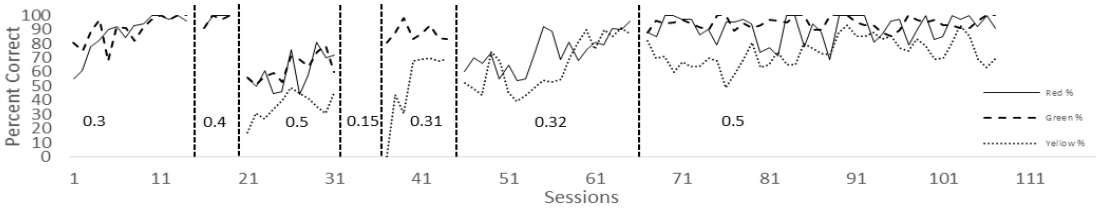


Figure Thirty Six 13.3 Condition 0.5 Accumulative Data

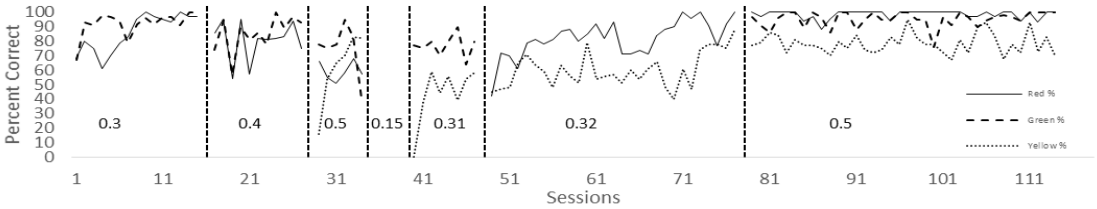


Figure Thirty Seven 13.4 Condition 0.5 Accumulative Data

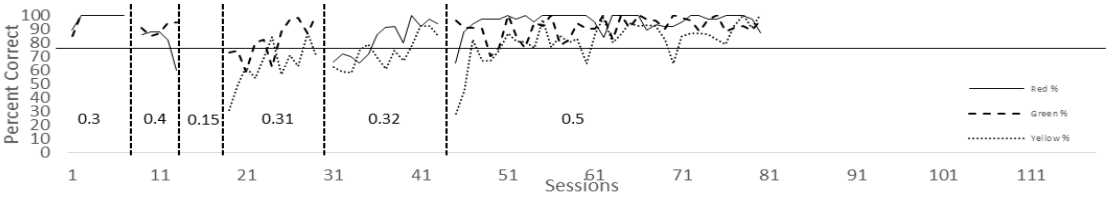


Figure Thirty Eight 13.5 Condition 0.5 Accumulative Data

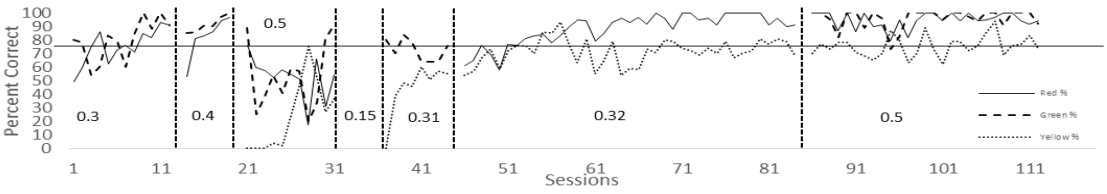


Figure Thirty Nine 13.6 Condition 0.5 Accumulative Data

Condition 0.5

The graphs show (*Figures 34-39)* the performance over the presentation of all three directional gratings. All subjects met the threshold of 75% correct over two consecutive days for entry into the Experimental Conditions apart from Bird 13.1 whose performance never met the requirements.

Data were collected on the percentage of correct responses over all three gratings in order to ensure that performance was maintained. Subjects were required to attain percentages on all three keys at or above 75% for two consecutive days. It was critical that before the main experimental conditions were run that sufficient subjects had acquired mastery of all three directions.

Video Observations

A GoPro HERO 4 was attached to a Perspex window over two Regular Plaid Probe experiment sessions in order to provide insight into the pecking and posture topographies for each of the subjects. Distance from screen, side-on vs. front-on viewing, pecking behaviours such as posture, height, frequency, and velocity were all considered. These chamber behaviour differences were observed to try and explain for any variance in the responding to plaid trials between subjects by determining an observational difference in these topographies before a statistical analysis was completed.

Subjects varied in height, peck frequency, and peck velocity but it was concluded that there were no clear observational differences in the chamber behaviours between any of the subjects that would impact on their responding in terms of their ability to view the trials unimpeded.

Experiment One

Experiment One remained the same as Condition 0.5 but included the addition of probe trials. Probe trials were presentations of the plaid stimulus movies (summed 45° and 135° gratings) and were presented pseudo-randomly once every ten regular trials. A peck within the peck radius resulted in the presentation of all three response keys. The only difference is that a response on any of the response alternatives never resulted in reinforcement. This was necessary as we were trying to infer what the subject perceived rather than influence the responding.

The experiment was concluded automatically after 600 total trials which included an average probe total of approximately 60. Data were recorded on probe trial responses along with regular trials as a cumulative percentage in order to monitor that performance was maintained at an appropriate level.

Experiment Two

Experiment Two was an exact replication of Experiment One apart from the probe trials which were replaced with a square stimulus as opposed to a circular stimulus. This novel plaid was slightly larger than the regular plaids (within circular apertures) but had all of the same parameters (refresh rate, contrast etc.) as the other movie file used in the experiments. The reason for the modified plaid stimulus is discussed further in the discussion sections.

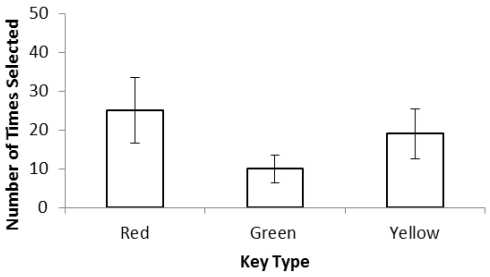


Figure Forty Experiment One: 13.2 Total Responses for Probe Trials

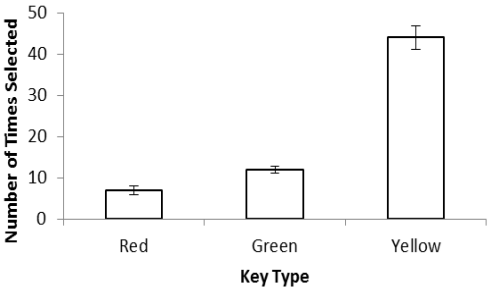


Figure Forty One Experiment One: 13.3 Total Responses for Probe Trials

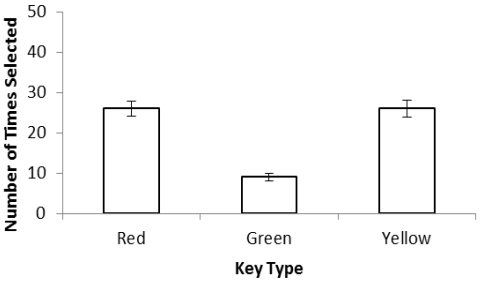


Figure Forty Two Experiment One: 13.4 Total Responses for Probe Trials

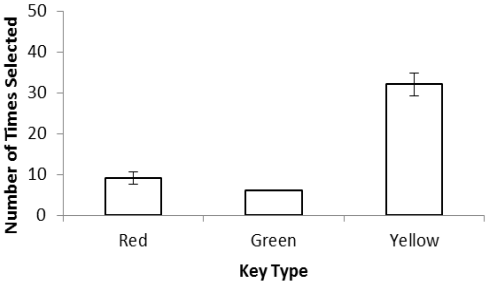


Figure Forty Three Experiment One: 13.5 Total Responses for Probe Trials

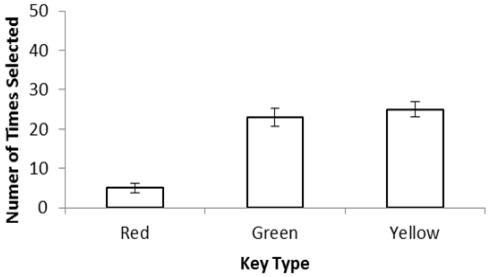


Figure Forty Four Experiment One: 13.6 Total Responses for Probe Trials

EXPERIMENT 1 - Plaid Probes

Results

Birds 13.3 and 13.5 (Figs. 41& 43) show a high level of yellow responses which suggest that these two birds may have perceived upwards motion on some level but we cannot be sure that this was not a bias for the yellow response key. The fact that the other three birds (Figs. 40, 42 & 44) appear to share their responding more evenly across the response alternatives suggest that they do not perceive any upwards motion.

Five out of six birds reached the criterion for inclusion in Experiment 1. The experiment involved the maintenance of mastery over the three grating types but included a plaid probe on average every 10 trials. Selection of the yellow key on probe trials indicates that the subject perceives upwards movement at 90°. Selection of either side keys during a probe trial suggests that the subject does not perceive upwards movement and instead perhaps the movement of the separate gratings making up the plaid and moving at either 135° or 45° directions. Responses may also have been random or with a bias to one side.

A repeated measures ANOVA was conducted in order to determine whether there was a significant difference between the mean responses during probe trials over the three response alternatives between subjects. A high proportion of yellow responses during probe trials would suggest that the overall global plaid motion (90°) is being perceived by the bird and a higher number of responses on the side keys during probe trials suggest that it is not perceived.

Mauchly's test indicated that the assumption of sphericity had not been violated X^2 (2) = .464, p = .793. The results show that response type was not significantly affected by stimulus type (regular probes), F (2,8) = 3.936, p = .075.

The presentation of plaid probes did not result in a significant number of vertical (yellow key) responses. This suggests that the subjects were not able to reliably perceive the overall global motion of the plaid (90°). Instead, the birds may have perceived one or both of the gratings separately or evenly distributed their responses over all response keys to try and gain reinforcement.

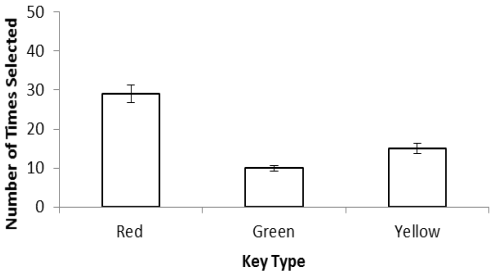


Figure Forty Five Experiment Two: 13.2 Total Responses for Probe Trials

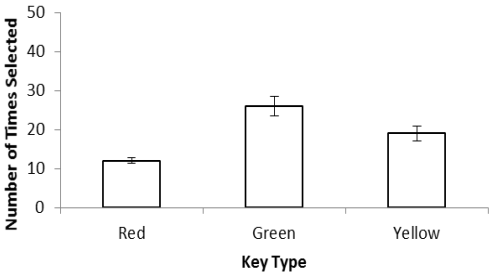


Figure Forty Six Experiment Two: 13.3 Total Responses for Probe Trials

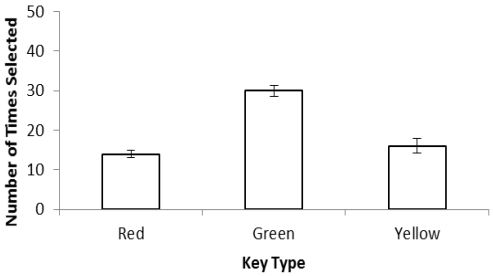


Figure Forty Seven Experiment Two: 13.4 Total Responses for Probe Trials

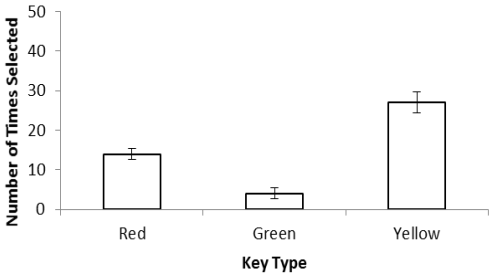


Figure Forty Eight Experiment Two: 13.5 Total Responses for Probe Trials

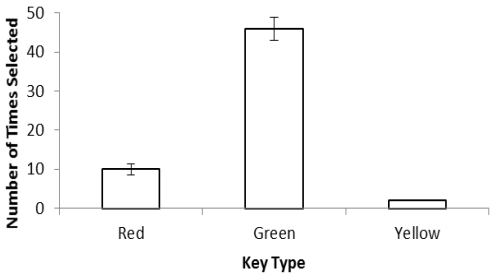


Figure Forty Nine Experiment Two: 13.6 Total Responses for Probe Trials

EXPERIMENT 2 - Square Plaid Probes

Results

Figures 45-49 show the overall responses during probe trials. The responses appear to be distributed relatively evenly across the three response alternatives apart from what appears to be a preferred response alternative for each bird characterised by larger amounts of responding. This is perhaps a product of the repeated presentations of probe trials resulting in what is almost a routine response to a particular key in order to move on to a trial which results in reinforcement. This may be illustrated by habitual responding to a preferred side key during the probe trials which results in a large number of probe responses to one particular key compared with the others. This theory is discussed further in the discussion section below.

There were a number of possible reasons why the birds did not respond to the overall global motion direction. They may not have been able to combine the two different grating directions, i.e., they do not have the same pattern motion processing abilities as humans. They may also see the stimuli very differently from us. The barber pole stimulus can be made to look as though it moves in a particular direction by changing the shape of the window that occludes the moving grating (Wuerger et. al., 1996). The theory is that humans use the points at which the gratings meet the aperture edges (endpoints or line terminators) to help decide the overall motion direction; apertures that are wider horizontally than vertical have more terminators moving in the horizontal directions than vertical

and this explains why humans tend to see overall motion in this type of aperture as horizontal.

The plaid stimuli used in this current experiment used a circular aperture. If the birds relied on the motion of the grating line endpoints (terminators) to determine the overall motion direction then they would experience a range of possible directions because the terminators along the circular aperture move in many directions. In an attempt to see if birds were using line terminators to determine the direction, the plaid was presented in a square aperture which has many upward moving terminators along its two vertical edges. This should increase the chances that the birds respond to the global vertical motion of the plaid.

The same five birds were then exposed to a modified version of the experiment in which the circular plaid was replaced with a square plaid. Again, selection of the yellow key indicates that the subject perceives the stimuli as a plaid with movement at 90°. Selection of either side keys suggests that the subject does not perceive the global motion percept and may just respond to singular gratings as opposed to the summed gratings, or with a bias to one side.

A repeated measures ANOVA was conducted in order to determine whether there was a significant effect between the mean responses during probe trials over the three response alternatives between subjects.

Mauchly's test indicated that the assumption of sphericity had not been violated X^2 (2) = 2.265, p = .322. The results show that response type was not significantly affected by stimulus type (square probes), F (2,8) = .449, p = .583.

The additional vertical motion of the terminators along the edges of the square aperture did not significantly increase the number of vertical (yellow key)

responses. This suggests that the motion of the endpoints or terminators in the moving plaid (or grating) stimuli was not a strong source of direction information for the birds.

Discussion

This thesis aimed to achieve two goals. Develop a reliable method in order to achieve the desired discriminative performance from the subjects using a range of behavioural analytic techniques. By utilising a behavioural analytic approach we trained the subjects for the task by constantly adjusting our methods to fit the performance requirements. By developing a reliable method of training this thesis sought to achieve the second goal: teaching and maintaining performance at a level high enough to be able to present the plaid probe trials in the 135°, 90°and 45° direction discrimination task described above. By achieving the required subject performance and presenting 'plaid' probe trials, we hoped to determine whether or not the domestic chicken has the ability to overcome the aperture problem.

The chickens in this study were clearly able to discriminate direction of movement based on their responding during the initial single grating conditions. The results of the first experimental condition (regular plaid probes) show that the subjects do not have the ability to solve the aperture problem. High percentages of responses on side keys (red and green) suggest that the birds either had a bias for one side key or responded randomly.

The second experimental condition (square plaid probes) was designed to try and increase the aperture problem cues by making the edges less ambiguous and increasing the disparity between the outside of the plaid and the background. Again, the subjects did not have the ability to solve such global motion estimation problems. Some of the possible reasons for these conclusions are mentioned below.

Structural Factors

The visual systems of a chicken brain may differ structurally from a human in such a way that specialised cells for locating edges, line terminators, and direction are not enough or do not exist as they do in the mammalian visual system. Although there is thought to be a similar motion detecting system between mammals and members of the avian family, perhaps chickens do not perceive such detailed information as other species do (Baron et. al., 2007; Bingman et. al., 2008; Karten et. al., 1973; Macko & Hodos, 1984).

Optical Factors

Differences between a human eye and a chicken eye are many. Chickens are equipped with laterally positioned eyes that contain two foveae as opposed to our one. As previously suggested perhaps the two foveae serve different viewing functions (Dawkins 1995, 1996, & 2002; Friedman, Vuong, & Spetch, 2009; Maldonado et. al., 1988). The binocular field of view may be associated with locating food and pecking behaviours while lateral viewing may be used for more movement based perception (Dawkins 1995, 1996, 2002; Maldonado et. al. 1988).

A chicken's stereo vision is limited due to the placement of the eye on the head therefore there is a possibility that this impacted on their performance during the experiment. Research suggests that birds with laterally positioned eyes have minimal amounts of binocular overlap which impacts on their binocular visual abilities (Dawkins, 1995; Dawkins & Woodington, 2000; Michael, Lowel, & Bischof, 2015). The video footage obtained via GoPro HERO 4 showed that the

subjects were generally viewing the stimuli front on. Their limited stereo vision could well have an impact on the perception of the moving gratings.

Chamber Behaviour

We are also aware that the experiment presents a rather laboratory-based environment to the subjects whose motion perception is generally specialised for viewing either danger, or points of interest (Bischof, 1999). A chicken's behaviour in a natural environment may vary from the responses that we observed in the chamber. Every aspect of the chamber and experimental presentation was man-made and didn't seek to replicate the type of motion that a chicken may have experienced before.

GoPro HERO 4 footage was taken to determine if there was less time spent viewing the plaid stimulus as reinforcement could be attained without responding accurately to what was perceived. The recordings did not show any obvious observational differences between subject behaviour that could account for the variance in responding although footage was only taken over two and a half experimental sessions and may not represent typical responding during previous or following sessions.

Training Process

The training process may have influenced the outcome of the behaviours. The subjects had experience in an operant chamber before but the infrared screen and stimuli were all novel. Although efforts were made to reduce and prevent bias,

previous experience with reinforcement on a particular key may have influenced the behaviours. The way new stimuli were added to the various conditions was also done relatively rapidly and in one case resulted in us having to retrain other aspects of the desired behaviours (original condition 0.5, see *Table One).*

Condition 0.3 taught subjects 0° and 180° associations with response keys rather than 45° and 135° which were used in the rest of the training conditions and ultimately the experiments. This was done in order to ascertain that the subjects were determining their cues based on the direction of movement (motion cues) rather than the orientation of the bars (orientation cues) during the presentation of grating stimuli. The 0° and 180° grating stimuli were identical except for their motion direction as the bars are oriented vertically in both cases. The association with a response key had to be made based on the direction it was moving. If we had begun the training conditions with 45° and 135° grating stimuli then we would not have been able to determine whether the subjects were responding based on the orientation of the grating bars or the direction of movement as these two stimuli vary, unlike the Condition 0.3 stimuli. A limitation has been discussed that queries whether it would have been useful to repeat the initial training method Condition 0.3 but adjust the stimuli to include the 90° grating stimuli (yellow key) moving upwards and a 90° grating stimuli moving downwards (novel-coloured key). Therefore, the orientation of the bars would have been identical for both stimuli (horizontal) meaning the cues would have had to have been determined from the direction of movement. The subjects may not have been able to relay feedback to us reliably during probe trials because it was a novel stimulus. By providing the downwards alternative perhaps the subjects may have been better equipped to respond to this novel stimulus.

Strengths & Weaknesses of Experimental Conditions

The overall goal for the research was not so much to determine whether or not chickens can determine global motion direction and to overcome the aperture problem, but rather to provide a reliable training system that quickly gets them up to the performance levels required to answer the vision-based questions. By practising behaviour analytical techniques in our training conditions we were able to actively modify the conditions as we went in order to provide the best outcomes for the experimental plan. Once performance was adequate we were ready to present probe trials. This probe consisted of the summed angled gratings, which we as humans perceive moving upwards at 90°. The results for Experiment 1 showed varying responses between subjects but this was not significant. Overall, the conclusion was that chickens do not see the global upwards motion of the plaids as we do.

Experiment 2 was designed in order to try and present a less ambiguous plaid pattern by showing a square plaid. The increase in vertical edges was supposed to try and increase the opportunity for solving the aperture problem. Some species have specialised end-stopped cells which could be used to follow the end points of the grating patterns to help estimate the global motion of the pattern. A vertical sided aperture (window) has more upward moving features and this should have led to more 90° responses. Again, this did not occur and the subjects had no preference for the upward direction.

A weakness in this experimental process was the multiple presentations of probe trials. Experiment 1 was conducted twice before video footage was taken on a further two days. This was because the experiment only consisted of 60 probe

trials amongst an average of approximately 600 regular trials. This lasted around six days depending on the subject's response rate. This number was selected as the experimental parameters were loosely based on pigeon based research that involved presenting the waterfall effect (Xiao & Gunturkun, 2008). By this stage it was possible that subjects were not responding desirably as the probe trials did not result in reinforcement. This means that the subjects may have selected their responses randomly in order to move on and gain reinforcement from a regular trial. Over exposure to the probes may have affected the subject's performance which is why data from the initial experiment has been included for statistical analysis.

Experiment 2 sought to push the subjects to solve the aperture problem by using square plaid probe trials. This experiment was presented two times but again the first experiment's data was obtained for statistical analysis. By conducting Experiment 2 after previous exposure to high amounts of Experiment 1 probes, performance during these trials may have been affected. Although the probe stimulus was novel, the subjects may have quickly associated the probes trials with no reinforcement, again influencing the overall performance during these sessions. Forethought had been given to the fact that probe trials did not result in reinforcement which is why the probe frequency was selected as it was. The decision to present small amounts of probe trials amongst large amounts of reinforcing trials was decided as the most appropriate way to conduct this research.

Conclusion

In conclusion, domestic chickens are able to make directional judgements based on motion cues but are not able to solve the aperture problem as humans and nonhuman primates do. When provided with a method in which to relay feedback, chickens are able to accurately respond to three moving grating directions accurately.

By providing a procedure in which to achieve this level of responding this thesis hopes to add an effective behavioural analytic process to current research in which other researchers can utilise to achieve the desired response behaviours relevant to their research. We were able to design and actively modify our training techniques to attain performance from our subjects that was at a level high enough to present our experimental conditions. We were able to maintain this performance in order to obtain data during the probe trials which led us to reasonable inference into whether or not domestic chickens face the aperture problem.

This study provided us with a better understanding of how to train and use domestic chickens for experiments testing their visual capabilities. We were able to determine whether they could reliably indicate grating movement direction, how much training was required to achieve adequate performance levels and what modification to the experiment was appropriate for the next level of learning.

References

Baird, A. A. (2010). *Think psychology.* NJ, USA: Prentice Hall.

Baron, J., Pinto, L., Dias, M. O., Lima, B., & Neuenschwander, S. (2007). Directional responses of visual wulst neurones to grating and plaid patterns in the awake owl. *European Journal of Neuroscience, 26*(7), 1950-1968. doi:http://dx.doi.org.ezproxy.waikato.ac.nz/10.1111/j.1460-9568.2007.05783.x

Beer, A. L., Watanabe, T., Ni, R., Sasaki, Y., & Andersen, G. J. (2009). 3D surface perception from motion involves a temporal-parietal network, *European Journal of Neuroscience, 30,* 703-713. doi:10.1111/j.1460-9568.2009.06857.x

Bingman, V. P., Gasser, B., & Colombo, M. (2008). Responses of pigeon (*Columba livia*) Wulst neurons during acquisition and reversal of a visual discrimination task. *Behavioral Neuroscience, 122*(5), Oct 2008, 1139-1147. doi.org.ezproxy.waikato.ac.nz/10.1037/a0012586

Bischof, W. F., Reid, S. L., Wylie, D. W., & Spetch, M. L. (1999). Perception of coherent motion in random dot displays by pigeons and humans. *Perception & Psychophysics, 61*(6), 1089-1101.

Blake, R., & Sekuler, R. (2006). *Perception* (5th ed.). NY, USA: McGraw-Hill

Cheadle, S. W., & Zeki, S. (2014). The role of parietal cortex in formation of colour and motion based concepts, *Frontiers in human neuroscience, 8,* 535. doi: 10.3389/fnhum.2014.00535

Colman, A. (2015). Psychophysics. In A Dictionary of Psychology. : Oxford University Press. Retrieved 10 Mar. 2016, from http://www.oxfordreference.com.ezproxy.waikato.ac.nz/view/10.1093/acref/9780199657681.001.0001/acref-9780199657681-e-6848.

Dawkins, M. S. (1995). How Do Hens View Other Hens? The Use of Lateral and Binocular Visual Fields in Social Recognition, *Behaviour*, *132*(7/8), 591–606. Retrieved from http://www.jstor.org.ezproxy.waikato.ac.nz/stable/4535284

Dawkins, M. S. (1996). Distance and Social Recognition in Hens: Implications for the Use of Photographs as Social Stimuli. *Behaviour*, *133*(9/10), 663–680. Retrieved from http://www.jstor.org.ezproxy.waikato.ac.nz/stable/4535388

Dawkins, M. S. (2002). What are birds looking at? Head movements and eye use in chickens. *Animal Behaviour*, *63*(1), 991-998. doi:10.1006/anbe.2002.

Dawkins, M. S., & Woodington, A. (2000). Pattern recognition and active vision in chickens. *Nature*, *403*(6770), 652-5. doi:http://dx.doi.org/10.1038/35001064

Friedman, A., Vuong, Q. C., & Spetch, M. L. (2009). View combination in moving objects: The role of motion in discriminating between novel views of similar and distinctive objects by humans and pigeons, *Vision Research, 49* (6), 594-607. doi.org/10.1016/j.visres.2009.01.019.

Gharaei, S., Tailby, C., Solomon, S. S., & Solomon, S. G. (2013). Texture-dependent motion signals in primate middle temporal area, *The Journal of Physiology, 591* (22), 5671-5690. doi.org/10.1113%2Fjphysiol.2013.257568

Goldstein, E. (2002). *Sensation and Perception 6th ed*. Boston, MA: Wadsworth

Hubel, D. H., & Wiesel, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *Journal of Physiology, 195*, 215-243.

Hulme, O. J., & Zeki, S. (2006). The Sightless View: Neural Correlates of Occluded Objects, *Cerebral Cortex, 17,* (5), 1197-1205. doi:10.1093/cercor/bhl031

Karten, H. J., Hodos, W., Nauta, W. J. H., & Revzin, A. M. (1973). Neural connections of the "visual Wulst" of the avian telencephalon: Experimental studies in the pigeon and owl. *Journal of Comparative Neurology, 150,* 253-278.

Kourtzi, Z., Krekelberg, B., & van Wezel, R. J. A. (2008). Linking form and motion in the primate brain, *Trends in Cognitive Sciences, 12* (6), 230-236. doi.org.ezproxy.waikato.ac.nz/10.1016/j.tics.2008.02.013

Kral, K. (2003). Behavioural–analytical studies of the role of head movements in depth perception in insects, birds and mammals. *Behavioural Processes, 64*, 1-12. doi:10.1016/S0376-6357(03)00054-8

Macko, K. A., & Hodos, W. (1984). Near-field acuity after visual system lesions in pigeons: I. Thalamus. *Behavioural Brain Research, 13,* 1-14.

Maldonado, P. E., Maturana, H., & Varela, F. J. (1988) Frontal and Lateral Visual System in Birds, *Brain Behaviour Evolution, 32* (1), 57-62. doi:10.1159/000116532

Martin, G. R., & Katzir, G. (1999). Visual Fields in Short-Toed Eagles, *Circaetus gallicus* (Accipittridae), and the Function of Binocularity in Birds, *Brain, Behaviour and Evolution, 53* (2), 55-66. Retrieved from http://ezproxy.waikato.ac.nz/login?url=http://search.proquest.com/docview/232153754?accountid=17287

Michael, N., Löwel, S., Bischof, H. J. (2015). Features of the Retinotopic Representation in the Visual Wulst of a Laterally Eyed Bird ,the Zebra Finch (Taeniopygiaguttata). *PLoSONE, 10*(4), 1-26. doi:10.1371/journal.pone.0124917

Movshon, J. A., & Adelson, E. H. (1984). The perception of coherent motion in two-dimensional patterns, *Computer Graphics, 18* (1), 23-24. doi.org.ezproxy.waikato.ac.nz/10.1145/988525.988531

O'Brien, J., & Johnston, A. (2000). When texture takes precedence over motion in depth perception. *Perception, 29,* 437-452. doi:10.1068/p2955

Pack, C. C., Livingstone, M. S., Duffy, K. R., & Born, R. T. (2003). End-Stopping and the Aperture Problem: Two-Dimensional Motion Signals in Macaque V1, *Neuron, 39* (4), 671-680. doi:10.1016/S0896-6273(03)00439-2

Piers, D. L. H., & Livingstone, M. S. (2006). V1 Partially Solves the Stereo Aperture Problem, *Cerebral Cortex, 16* (9), 1332-1337. doi:10.1093/cercor/bhj077

Pinto, L., Dias, M.O., Lima, B., Neuenschwander, S. & Baron, J. (2006). Response of visual Wulst neurons to plaid patterns in the burrowing owl. *XXI Reunia˜o Anual Da Federac¸a˜o de Sociedades Brasileiras de Biologia Experimental, 5*(125).

Pinto, L., Dias, M.O., Lima, B., Neuenschwander, S. & Baron, J. (2007) Steady-state and dynamical aspects of component direction selectivity in the visual Wulst of awake owls. *II International Neurosciences Symposium of the IINN, Natal, 156.*

Prum, R. O. (2014). Interspecific social dominance mimicry in birds. *Zoological Journal of the Linnean Society, 172* (4), 910–941. doi: 10.1111/zoj.12192

Schlack, A., & Albright, T. D. (2007). Remembering Visual Motion: Neural Correlates of Associative Plasticity and Motion Recall in Cortical Area MT, *Neuron, 53* (6), 881-890. http://dx.doi.org/10.1016/j.neuron.2007.02.028

van Ee, R., & Anderson, B. L. (2001). Motion, direction, speed and orientation in binocular matching, *Nature, 410* (6829), 690-694. doi:http://dx.doi.org/10.1038/35070569

Wuerger, S., Shapley, R., & Rubin, N. (1996). On the visually perceived direction of motion by Hans Wallach: 60 years later, *Perception, 25*, 1317-1367

Wylie, D. R. W., Bischof, W. F., & Frost, B. J. (1998). Common reference frame for neural coding of translational and rotational optic flow. *Nature, 392*(6673), 278-82. doi:http://dx.doi.org/10.1038/32648

Xiao, Q., & Frost, B. J. (2013). Motion parallax processing in pigeon (Columba livia) pretectal neurons. *European Journal of Neuroscience, 37,* 1103–1111. doi:10.1111/ejn.12115

Xiao, Q., & Güntürkün, O. (2008). Do pigeons perceive the motion aftereffect? A behavioral study, *Behavioural Brain Research, 187* (2), 327-333. doi.org/10.1016/j.bbr.2007.09.026

Zahar, Y., Wagner, H., & Gutfreund, Y. (2012). Responses of Tectal Neurons to Contrasting Stimuli: An Electrophysiological Study in the Barn Owl. *PLoS ONE 7*(6). doi:10.1371/journal.pone.0039559.

Zeki, S., & Stutters, J. (2013). Functional specialization and generalization for grouping of stimuli based on colour and motion, *NeuroImage, 73*, 156-166. doi:http://dx.doi.org/10.1016/j.neuroimage.2013.02.001